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Heterosis and Combining Ability of Amylose Content and Amylographic Breakdown Viscosity in Milled Rice(*Oryza sativa* L.)[1]

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Abstract: Heterosis and combining ability for two quality paramenters, amylose content and amylographic breakdown viscosity, of rice grain were studied in 30 cross combinations involving six entries of rice (*Oryza sativa* L.). Data indicated that heteroses over their midparent (MP) or higher-parent (HP) were observed. The extent of heteroses over their MP or HP varied from cross to cross for these two evaluated quality parameters. As to amylose content, heterosis over their MP almost appeared to be in positive direction, however, heterosis over their HP were almost in negative direction. In contrast, heteroses over their either MP or HP almost were in negative directions for amylographic breakdown viscosity. High significant differences were observed for mean squares of general combining ability (GCA) and specific combining ability (SCA) of these two evaluated quality parameters. Futhermore, the mean square of GCA was very larger than that of SCA. The ranking of the parents according to GCA effects closely corresponded to their ranking according to parents means. It minght conclude that despite of issues indicated in discussion in this paper, gene action for amylose content and amylographic breakdown viscosity was similar and mainly additive, although dominance effect was also involved; reciprocal effect upon two evaluated quality parameters could be ignored; and parent choice based upon GCA effects would be similar to selection based upon parent means.

Key words: Heterosis, Combining ability, Amylose content, Amylographic breakdown viscosity, *Oryza sative* L.

INTRODUCTION

Amylose content of milled rice, a chemical property of rice, is usually considered to be one of the most important attributes for predicting cooking, eating, and processing qualities

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[11,17,22,24] Cultivars with low amylose content cook moist, sticky, and tender. Cultivars with high amylose content cook dry and fluffy and usually become hard upon cooling. Whereas, those with intermediate amylose content cook tender and fluffy and do not become hard upon cooling[9,12]. Thus, cultivars with different amylose content are preferred by various consumers.

Amylograph pasting profile of milled rice, a physical property of rice, determined with the Barbender Visco/Amylograph, shows appreciable differences among cultivars of the known cooking, eating, and processing behavior. For example, a low amylographic breakdown viscosity is indicative of low loss of solids and little splitting and frying of edges and ends in canning[22]. Thus, Webb and Stermer[22] considered that amylographic breakdown viscosity is particularly useful in evaluating cultivars of superior parboil-canning and quick-cooking parameters. In contrast, Scientists in Japan found that the preferred Niigata rice have a higher peak viscosity and greater breakdown viscosity than those of the nonsticky rice and that the flaky rices grown in Hokkaido have lower peak and breakdown viscosities and higher consistency than those of good quality sticky rices grown in Honsu[20]. Published data from Taiwan, ROC. clearly and definitely indicated highly significant correlations between amylographic viscosity measurements and preferred eating quality[14]. Thus, that amylographic breakdown viscosity could be selected as an index factor for sticky palatability evaluation was recommended by the Oriental rice scientists[14,20].

Rice quality preferred in the word rice market is so highly sophisticated[5,10] that it is vitally important in now and / or future rice breeding program that breeding new rice cultivars are more diverse and innovative in production and utilization and in cooking, eating, and processing to meet the needs of different consumers[3,4,15,23]. Therefore, comprehensive investigations on cooking, eating, and processing quality parameters are absolutely necessary for a breeding program with high priority on eating and processing qualities. The objectives of the present report was to provide some basic information about heterosis and combining ability of amylose content and amylographic breakdown viscosity of milled rice.

MATERIALS AND METHODS

Six indica rice entries, Rexmont, Guichow, Lemont, CI 9902, TCS 10, Toro II, representing an array of different levels of amylose content and amylographic breakdown viscosity as shown in Table 1 and Fig. 1, were used as the parents. All possible cross-combinations, including reciprocals, were made. The six parents and one set of F_1 hybrids, 30 combinations, were cultivated in a flooded paddy field at the Texas A&M University Agricultural Research and Extension Center near Beaumont, Texas, in a randomized complete block design with three replications. Each block consisted of 36 four-row plots. Each plot included 40 plants spaced at 30×30cm. Twenty plants from the two central rows of each plot were harvested and analyzed.

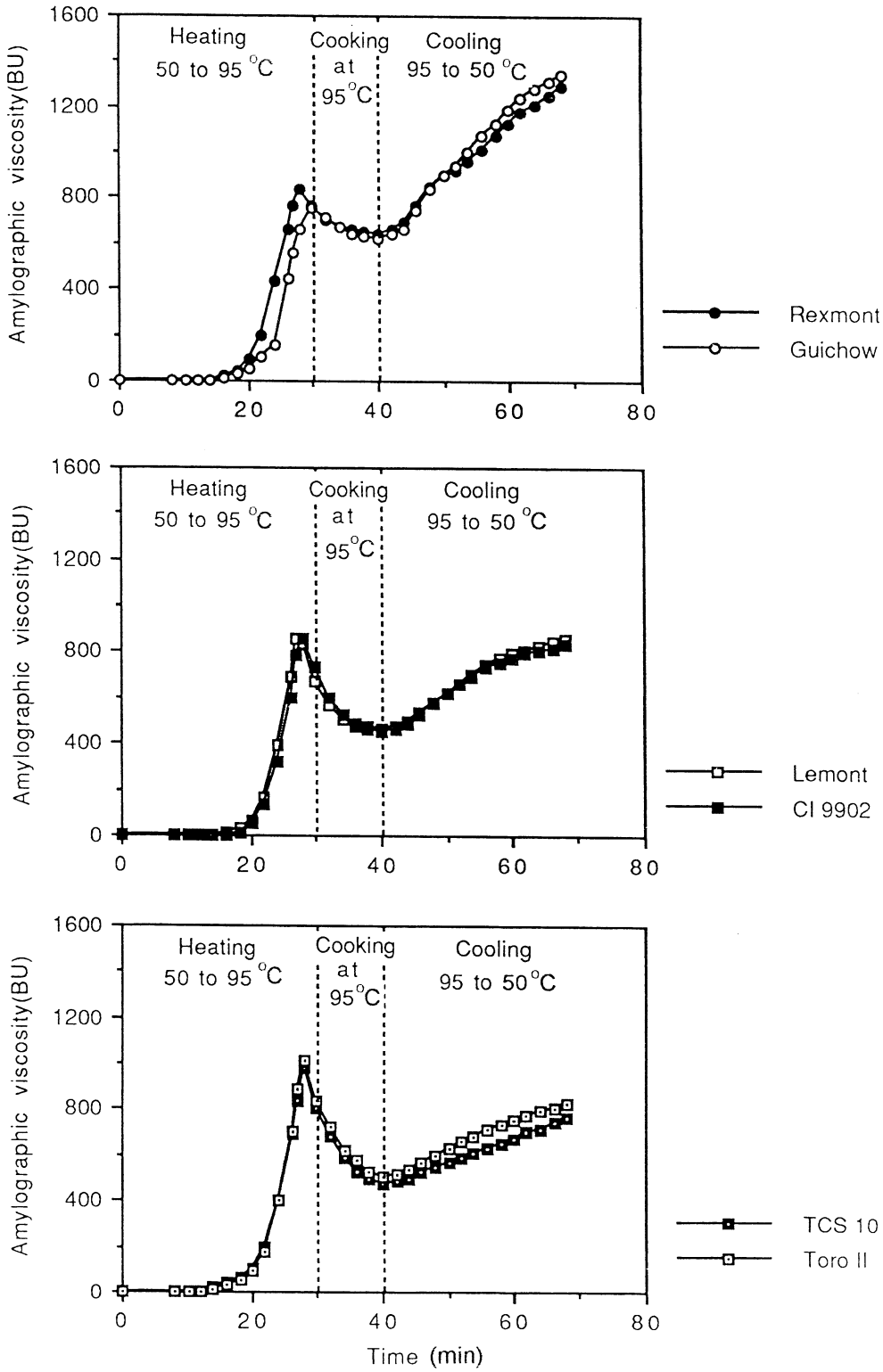

Fig. 1. Amylographic profiles of the six parents used in the diallel cross

Table 1. Mean values of amylose content and amylographic viscosity parameters of the six parental entries.

Parent	Amylose content	Amylographic viscosity (BU[z])		
	(%)	Peak	Hot-paste	Breakdown
Rexmont(P_1)	26.3	833	640	193
Guichow(P_2)	27.4	747	620	127
Lemont(P_3)	22.3	843	463	380
CI 9902(P_4)	22.6	853	470	383
TCS 10(P_5)	14.5	997	490	507
Toro II(P_6)	15.2	1,010	510	500

BU: Brabender Unit.

Amylose content of milled rice was analyzed by a totally automated system of amylose content innovated by Webb [21]. Amylographic pasting characteristics were determined by the method developed by Hailic and Kelly [7]. Combining ability components, general combining ability (GCA) and specific combining ability (SCA), were analyzed by the Method I, Model I of Griffing's diallel method, i.e., the parents, one set of F_1 hybrids are included in a model with fixed genotypic effects [6].

RESULTS

Heterosis of Amylose Content

Mean values of mid parents (MP), higher parents (HP), F_1 hybrids, heteroses over MP and HP for amylose content of milled rice of 30 combinations were presented in Table 2. As shown in Table 2, a total of 18 hybrids out of 30 combinations having significantly higher amylose content than their MP was observed. The extent of heterosis over MP varied from 4.7 (Toro II×Rexmont) to -1.5 (TCS 10×Toro II). It should be pointed out a tendency that the hybrids having significantly higher amylose content than their MP were found from the crosses between high or intermediate and low amylose content parents, except for TCS 10×Toro II combination a cross between two low amylose content parents, and Lemont×Rexmont combination, a cross between intermediate and high amylose content parents. On the other hand, a total of 7 hybrids out of 30 combinations had significantly lower amylose content than their HP, with a maximum decrease of -3.4 in TCS 10×Guichow combination. The fact that the hybrids with significantly lower amylose content than their HP were derived from the crosses between high or intermediate and low amylose content parents were also observed, except for Guichow×Lemont, a cross between high and intermediate amylose content parents.

Table 2. Mean performance of the thirty hybrids, mid-parent (MP), higher-parent (HP), and expression of heterosis for amylose content in crosses of six rice entries.

Cross	hybrid	MP	HP	Heterosis	
				MP	HP
Rexmont×Guichow	27.5	26.9	27.4	0.6	0.1
Rexmont×Lemont	25.4	24.3	26.3	1.1	−0.9
Rexmont×CI 9902	25.7	24.5	26.3	1.3	−0.6
Rexmont×TCS 10	23.3	20.4	26.3	2.9**	−3.0**
Rexmont×Toro II	25.1	20.8	26.3	4.3**	−1.2
Guichow×Lemont	25.7	24.9	27.4	0.8	−1.7*
Guichow×CI 9902	26.2	25.0	27.4	1.2	−1.2
Guichow×TCS 10	24.6	21.0	27.4	3.6**	−2.8**
Guichow×Toro II	25.3	21.3	27.4	4.0**	−2.1*
Guichow×Rexmont	27.9	26.9	27.4	1.0	0.5
Lemont×CI 9902	23.0	22.5	22.6	0.5	0.4
Lemont×TCS 10	20.9	18.4	22.3	2.5**	−1.4
Lemont×Toro II	22.2	18.8	22.3	3.4**	−0.1
Lemont×Rexmont	26.2	24.3	26.3	1.9**	−0.1
Lemont×Guichow	26.0	26.9	27.4	−0.9	−1.4
CI 9902×TCS 10	20.9	18.6	22.6	2.3**	−1.7*
CI 9902×Toro II	21.3	18.9	22.6	2.4**	−1.3
CI 9902×Rexmont	25.8	24.5	26.3	1.3	−0.5
CI 9902×Guichow	26.1	25.0	27.4	1.1	−1.3
CI 9902×Lemont	22.9	22.5	22.6	0.4	0.3
TCS 10×Toro II	14.4	15.9	15.2	−1.5*	−0.8
TCS 10×Rexmont	23.2	20.4	26.3	2.8**	−3.1**
TCS 10×Guichow	24.0	21.0	27.4	3.0**	−3.4**
TCS 10×Lemont	21.2	18.4	22.3	2.8**	−1.1
TCS 10×CI 9902	21.0	18.6	22.6	2.4**	−1.6
Toro II×Rexmont	25.5	20.8	26.3	4.7**	−0.8
Toro II×Guichow	24.7	21.3	27.4	3.4**	−2.7*
Toro II×Lemont	21.2	18.8	22.3	2.4**	−1.1
Toro II×CI 9902	21.8	18.9	22.6	2.9**	−0.8
Toro II×TCS 10	14.3	14.9	15.2	−0.6	−0.9

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

Heterosis of Amylographic Breakdown Viscosity

Table 3 presented the data in relation to mean values of mid parents (MP), higher parents (HP), F_1 hybrids, heteroses over MP and HP for amylographic breakdown viscosity of milled rice of 30 combinations. Significant heterosis over their MP was observed in 16 cross combinations in negative direction and in one case in a positive diredtion. The extent of heterosis varied from -214 BU (Brabender Unite, Guichow×Toro II combination) to 35 BU (CI 9902×Lemont combination). In contrast, it was found that a total 26 out of 30 combinations exhibited significant heterosis over HP in negative direction. A tendency that the hybrids with significantly negative heterosis over HP were derived from the crosses between high and low amylographic breakdown viscosity parents. Only two hybrid combinations with positive heterosis over HP were observed. These combinations were derived from the crosses between intermediate×intermediate breakdown viscosity parents, i.e., Lemont and CI 9902. However, the positive heterosis of breakdown viscosity in the two combinations were no significantly different from their HP.

Table 3. Mean performance of the thirty hybrids, mid-parent (MP), higher-parent (HP), and expression of heterosis for amylographic breakdown viscosity in crosses of six rice entries.

Cross	hybrid	MP	HP	Heterosis	
				MP	HP
Rexmont×Guichow	163	160	193	3	− 60**
Rexmont×Lemont	257	287	380	− 30	− 123**
Rexmont×CI 9902	303	288	383	15	− 80**
Rexmont×TCS 10	320	350	507	− 30	− 287**
Rexmont×Toro II	240	347	500	− 107	− 260**
Guichow×Lemont	217	254	380	− 37	− 163**
Guichow×CI 9902	237	255	383	− 18	− 146**
Guichow×TCS 10	193	317	507	− 124**	− 314**
Guichow×Toro II	100	314	500	− 214**	− 400**
Guichow×Rexmont	157	160	193	− 3	− 36
Lemont×CI 9902	393	382	383	11	10
Lemont×TCS 10	407	444	507	− 37*	− 100**
Lemont×Toro II	383	400	500	− 17	− 117**
Lemont×Rexmont	313	287	380	26	− 67**
Lemont×Guichow	223	254	380	− 21	− 157**
CI 9902×TCS 10	400	445	507	− 45**	− 107**
CI 9902×Toro II	387	442	500	− 55**	− 113**
CI 9902×Rexmont	303	288	383	15	− 80**
CI 9902×Guichow	220	255	383	− 35*	− 163**
CI 9902×Lemont	427	382	383	35*	34
TCS 10×Toro II	460	504	507	− 44**	− 47*
TCS 10×Rexmont	333	350	507	− 17	− 174**
TCS 10×Guichow	200	317	507	− 117**	− 307**
TCS 10×Lemont	413	444	507	− 31	− 94**
TCS 10×CI 9902	410	445	507	− 35*	− 97**
Toro II×Rexmont	227	347	500	− 120**	− 273**
Toro II×Guichow	107	314	500	− 207**	− 393**
Toro II×Lemont	400	440	500	− 60**	− 100**
Toro II×CI 9902	373	442	500	− 69**	− 127**
Toro II×TCS 10	473	504	500	− 31	− 27

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

Analysis of Variance of Griffing's Method I

The analysis of variance of the diallel table for these two quality parameters according to Griffing's Method I were presented in Table 4. Highly significant differences from the zero were observed for both GCA and SCA of two evaluated quality parameters. However, the mean square of GCA was very larger than that of SCA for these two quality parameters. The ratios of GCA mean squares to SCA mean squares of amylose content and amylographic breakdown viscosity were 16 : 1 and 17 : 1, respectively. The data suggested that the inheritance of two evaluated quality parameters was mainly conditioned by additive gene effect, although dominant gene effect was also involved. No significant differences were observed for reciprocal (maternal) effect in relation to the two quality parameters, indicating that maternal (cytoplasm) influence upon two evaluated quality parameters might be ignored in the entries used.

Table 4. Analysis of variance of general combining ability (GCA) and specific combining ability (SCA) for amylose content and amylographic breakdown viscosity in rice.

source	D.F.	Mean squares	
		Amylose content	Amylographic breakdown viscosity
GCA	5	78.87**	78,325**
SCA	15	5.43**	4,617**
RE	15	0.28	120
Error	70	0.26	139

** Significant at the 0.01 probability level.

Combining Ability of Amylose Content

Estimates of Griffing's GCA and SCA effects for each of the parents for amylose content were enumerated in Table 5. The contribution of the individual entries to hybrid amylose content was accomplished by comparing the GCA effects. As shown in Table 5, all of the entries evaluated in this six-parents diallel cross could be divided into three groups. Rexmont and Guichow which exhibited greater positive GCA effects; Lemont and CI 9902, small positive GCA effects; TCS 10 and Toro II, greater negative GCA effects. Furthermore, the ranking of the parents according to GCA effects closely corresponded to their ranking according to parent means (Table 1). Thus, choice of parents based upon GCA effects would be similar to selection based upon parent phenotype.

Table 5. Estimates of general combining ability (GCA) and specific combining ability (SCA) effects for amylose content in each parental entries.

Parent	GCA	SCA effect					
		P_1	P_2	P_3	P_4	P_5	P_6
Rexmont(P_1)	2.48	—	−1.92	−0.04	−0.07	1.30	2.32
Guichow(P_2)	2.84		—	−0.27	−0.02	1.90	1.60
Lemont(P_3)	0.30			—	−0.68	1.28	0.90
CI 9902(P_4)	0.35				—	1.13	0.70
TCS 10(P_5)	−3.35					—	−2.65
Toro II(P_6)	−2.45						—

SE(Gi)=0.13 ; SE(Gi−Gj)=0.21 ; SE(Sij)=0.31 ; SE(Sii−Sij)=0.59
SE(Sii−Sjk)=0.45 ; SE(Sij−Sik)=0.47 ; SE(Sij−Skl)=0.41

A total of seven out of 15 hybrids exhibited negative SCA effects. These seven hybrids, Rexmont×Guichow, Rexmont×Lemont, Rexmont×CI 9902, Guichow×Lemont, Guichow×CI 9902, Lemont×CI 9902, TCS 10×Toro II, were derived by crossing high×high, high×intermediate, low×low amylose content parents. Among these hybrids, hybrid TCS 10×Toro II had the lowest negative SCA effects, whereas, the values of SCA effects of hybrids Rexmont×Guichow, Rexmont×Lemont, Rexmont×Lemont, Rexmont×CI 9902, Guichow×

Lemont, Guichow×CI 9902, Lemont×CI 9902 were equal to zero, This confirmed that the amylose content of the hybrids from crossing high×high and high×intermediate parents were approximately equalto their MP and/or HP (Table 2). The remaining eight hybrids exhibiting positive SAC effects were produced by crossing high×Low amylase content parents.

Combining Ability of Amylographic Breakdown Viscosity

The contribution of the individual entries to hybrid breakdown viscosity was indicated by comparing the GCA (Table 6). Parents TCS 10 and Toro II, both with high amylographic breakdown viscosity (Table 1), exhibited greater positive GCA effects than parents Lemont and CI 9902 which also showed positive GCA effects. On the other hand, Guichow, a relatively low breakdown viscosity parent, showed lower negative GCA effect than Rexmont which also was a relatively low breakdown parent (Table 1). However, a fact that the ranking of the parents according to GCA effects very corresponded to their ranking according to parent means could be inferred. Stated in other words, choice of the parents base upon GCA effects would be similar to selection based upon parent phenotype.

As shown in Table 6, eight of the 15 hybrids exhibited negative SCA effects for high breakdown viscosity. These eight hybrids, Rexmont×TCS 10, Rexmont×Toro II, Guichow ×TCS 10, Guichow×Toro II, Lemont×TCS 10, Lemont×Toro II, CI 9902×TCS 10, and CI 9902×Toro II, were derived by crossing low×high and intermediate×high breakdown viscosity parents. Among these hybrids, hybrid Guichow×Toro II showed the greatest negative SCA effect. The remaining seven hybrid exhibiting positive SCA effects were derived by crossing low×low, low×intermediate, intermediate×intermediate, high×high parents. Among these seven hybrids, Rexmont×Guichow, a low×low combination, and TCS and Toro II, a high×high combination, showed the greatest positive SCA effects.

Table 6. Estimates of general combining ability (GCA) and specific combining ability (SCA) effects for amylographic breakdown viscosity in each parental entries.

Parent	GCA	SCA effect					
		P_1	P_2	P_3	P_4	P_5	P_6
Rexmont(P_1)	− 57.43	—	44.91	4.07	9.07	− 1.20	− 55.09
Guichow(P_2)	−137.41		—	5.74	14.07	−51.20	−105.09
Lemont(P_3)	41.76			—	16.57	−17.04	− 4.07
CI 9902(P_4)	41.76				—	−22.04	− 7.59
TCS 10(P_5)	75.37					—	45.46
Toro II(P_6)	65.93						—

SE(Gi)=3.11 ; SE(Gi−Gj)=4.82 ; SE(Sij)=7.10 ; SE(Sii−Sij)=13.63 ;
SE(Sii−Sjk)=11.81 ; SE(Sij−Sik)=10.78 ; SE(Sij−Skl)=9.64

DISCUSSION

Earlier experiments on heterosis were conducted almost for academic studies, and their results were of limited practical value. Thus, heterosis for rice, usually for grain yield, could not be exploited commercially. The recent discoveries of a cytoplasmic male sterility and genic fertility restoration system in rice, reported by several workers[19,18,1,13,25], seemed to have saved this problem and producing hybrid seed on commercial basis as reasonably low cast may be feasible. Up to now, commercial cultivation of hybrid rice is practical in some areas[25]. However, in modern world rice market, grain quality is a major concern. Thus, rice quality parameters instead of rice grain yield was mainly emphasized in this report.

There are issues in diallel analysis, in genetic expression of endosperm characterisitics and in samples for endosperm characteristics determination. Firstly, according to a Baker's review of the diallel literature, he pointed out that from a genetical point of view, two assumptions, independent distribution of genes in parents and epistasis, are critical in attempts to interpret the results of diallel analyses. He indicated that to assume that genes are distributed independently in the parents of a diallel cross is not a realistic assumption. Furthermore, there are conflicting reports as to whether or not of this assumption will result in biased estimates of GCA and SCA components of variance. Besides, epistasis affects estimates of GCA and SCA mean square, variance, and effects in an unpredictable manner [2]. In this study, six rice entries, representing an array of different levels of amylose content and amylographic breakdown vicoity were used as the parents and a diallel cross was made. Combining ability and heterois for two major quality parameters in relation to eating and processing quality were studied. Data from analysis of variance of the diallel table by Haymen[8] method unpresented in this paper indicated that the assumptions of independent distribution of genes in the parents and epistasis appeared to have failed for these two major quality parameters. Therefor, the Baker's issues in discussing the topic about combining ability had to be kept firstly in mind.

Secondly, genetic expression of endosperm characteristics is under triploid genetic control. Thus, compared with other quantitative plant characteristics, such as plant height, panicle length, etc., endoperm characteristics play three distinct nature. That is, there is theoretically a difference between reciprocal cross, i. e., dosage effect ; endosperms on plants of the early generations of a hybridized population represents next generation ; and an individual is a seed, not a plant. However, up to now, a satisfactory genetic model for such endosperm characteristics has not yet been developed[16]. The lack of proper genetic model has been an obstacle in studying the inheritance of endosperm characteristics. Thus, all of published genetic studies on endosperm characteristics followed the example of diploid genetic model, such as plant height and panicle length etc., including this paper. Besides, Kumar and Khush[12] argued that analyses of genetically heterozygous buck seed samples on plants provided biased information for the genetic study on endosperm characteristiocs, such as amylose content. In this study, genetically heterozygous F_2 buck seed sample on

individual F_1 plant was run for amylose content and amylographic breakdown viscosity. These might be the second issue in this paper and had to be also kept in mind.

From the results obtained, despite of issues mentioned above, it might conclude that gene action for amylose content and amylographic breakdown viscosity in this study was mainly additive, although dominance gene effect was also involved ; reciprocal (maternal) effect upon two evaluated endosperm characteristics could be ignored ; parent choice based upon GCA effects would be similar to selection based upon parent means

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白米直鏈澱粉含量與澱粉崩解黏度之雜種優勢與組合力[1]

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摘 要

以六親本所雜交的30個水稻組合，探討米粒直鏈澱粉含量與澱粉崩解黏度的雜種優勢與組合力。數據顯示，與中間親本及高親本等比較的兩類雜種優勢均存在，兩個被評估米質性狀的兩類雜種優勢的程度因組合而有不同。就米粒直鏈澱粉含量言，與中間親本比較的雜種優勢多爲正值，但與高親本比較的雜種優勢概成負值。反之，澱粉崩解黏度的兩類雜種優勢多呈負值。此兩被評估米質性狀的一般組合力與特殊組合力的均方均顯著，甚且，一般組合力的均方遠大於特殊組合力的均方。按一般組合力大小排序的親本歸級與依親本各該性狀之測定值行排列者相當。在不考慮著者在文中討論部分所論及有關胚乳性狀遺傳研究的爭議時，本研究可作如後推論：在供試水稻材料中，直鏈澱粉含量與澱粉崩解黏度等兩性狀之遺傳行爲相似，主要均由累加性效應來控制，惟，顯性效應亦存在；正反交效應似可忽視；依一般組合力大小來行親本選擇時，與按親本各該性狀之實測值的大小行選擇相類似。

關鍵詞：白米、直鏈澱粉含量、澱粉崩解黏度、雜種優勢、組合力。

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